

Macropod ecophysiology: a possible integration with ecological and evolutionary studies

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Abstract

The relevance of ecophysiological studies on macropod species is explored in the context of a Hutchinsonian model of the niche. Perturbations which bring about an equivalence between, or an approximation of the realized to the fundamental niche are shown to be associated with large-scale increases in population size due to the loss of normal stabilizing mechanisms such as predation and competition. These concepts are discussed in relation to the problem of conservation of insular species of macropods.

Introduction

When the late Harry Waring took up the post of Professor in Zoology at the University of Western Australia his professed goal was to initiate studies on marsupials. Shortly after his arrival he was introduced to the quokka and thereafter took this species to be the typical macropod upon which the study of marsupials was to be based.

In the first decade of Waring's work on the quokka he spent much of his time and energy inducing those with access to funds or other resources to support his dream of basing marsupial studies on this animal on Rottnest Island. I was present on a number of such occasions and invariably the response was: "Why support work here? You have only a single marsupial, and that not in a typical habitat." This comment was accompanied by the advice that what he should do was come to the East where there was a much greater variety of marsupials and a real study could be undertaken. The outcome of these encounters was usually that Waring gained some support and, as everyone knows, stayed to study and sponsor studies by others on the quokka.

Having this background in mind, it is useful now to see whether and how the original studies on the quokka have enabled an expansion to include other species, and particularly what generalisations might be made from such studies. The purpose of this paper is not to review what has been achieved but to indicate in broad outline where and in what manner marsupial studies might be related to developing ecological theory and ecology generally.

Aims of ecophysiological studies

The central question is to establish whether the implied criticism of the single-species approach was valid or whether the study did allow for predictions and generalisations to flow to other species and so lead to broadly interpretative concepts or relate such to concepts raised in connection with other situations. Of course such generalisations require that some theoretical basis be established from which testable predictions and generalisations can be made. Prediction is likely to be more successful in so far as one departs from a mere recital of species differences and similarities and develops an hypothesis bearing a relationship to common environmental conditions.

In this regard one of the ubiquitous events of the environment in Australia is and has been the

progressive influence of desert and drought on the fauna. It is noteworthy that the environment of Rottnest Island is markedly different from the habitat occupied by the quokka on the mainland of Western Australia, and if one is interested in marsupials as a unique Australian biological entity or in the response of marsupials to drought, then the quokka on Rottnest is equally suitable regardless of whether it is the sole inhabitant of the island or not.

The early work carried out in the 1950's in Waring's laboratory was either related to reproductive physiology or physiological ecology (Bartholomew 1956, Bentley 1956, Moir *et al.* 1954, Moir *et al.* 1956). Subsequently a great many workers have used quokkas and a number of other species of macropods of various sizes as subjects of ecophysiological studies. Thus there is now a large body of information on the ecophysiological performance of a range of macropods. These studies fall broadly into one or the other of the following:

- (i) The physiological responses of macropods to ecological or field-induced stresses, e.g. urine volumes, electrolytes and urea in urine and plasma under conditions of electrolyte loading or water or heat stress, or urea recycling under conditions of inadequate diet (Kinnear *et al.* 1968, Purohit 1971, Main 1970, Kinnear and Main 1975, Hume and Dunning 1979).
- (ii) The physiological responses of macropods to stresses administered in the laboratory which are believed to be a realistic representation of field conditions. In the laboratory situation care is taken to see that the experimental animal is denied any opportunity to avoid the stressful situation by behavioural means. Such studies have encompassed regulation of body temperature under heat or cold stress, nitrogen balance with diets of various qualities or presented under conditions of heat or cold stress or water deprivation (Bartholomew 1956, Dawson and Bennet 1971, Brown 1969, Brown and Main 1967, Prince 1976).
- (iii) The physiological mechanism of response to field conditions or laboratory conditions presented to mimic field situations, such as the rôle of endocrine glands in initiating and sustaining the animal's responses e.g. pituitary, adrenal and kidney responses to

water deprivation or electrolyte loading or adrenal function in mobilizing tissue catabolism in starvation (Bradshaw *et. al.* 1975, McDonald 1977, McDonald and Bradshaw 1977, Miller and Bradshaw 1979).

Adaptation and persistence of macropods

While the studies have been progressing for a number of years in several laboratories, it is still true to say that relative to the total number of macropod marsupials, only a few species have been examined and none has been subjected to a complete ecophysiological analysis. We are thus left to ponder two questions. One is: are the species that have been accessible and amenable to study, the appropriate ones for making generalisations which are badly needed now that so many species require conservation and management in reservations? The second is: given that ecophysiological studies tell us what an animal can tolerate and how it does so in terms of physiological mechanisms, where do such studies fit in terms of ecological and evolutionary theory, i.e. what is their present function and how did they arise in the past? The possible answers to these questions are pursued below.

In many respects macropod marsupials appear to be in no way inferior to their herbivorous eutherian counterparts. On Rottneest Island the quokka occupies a habitat that would be quite unpredicted from its mainland occurrence, yet it and with few exceptions other marsupials have been unable to maintain their abundance in the face of agricultural and pastoral development on the mainland.

There is thus a paradox: on the one hand it is clear as the result of ecophysiological analysis that many species have well-developed physiological capacities to handle environmental stresses imposed by heat, water deprivation and low quality diet. In many cases the range of responses far exceeds what the animal may be called upon to perform for survival in nature. In this sense they are well-adapted to the environment in which they live.

On the other hand a number of species have declined in range and abundance (Lundelius 1963, Baynes 1980) since the advent of European man in Australia. A test of being adapted is to survive as an individual and persist as a population; in this sense they are unadapted to the new circumstances or at least their adaptations are not relevant to the changed conditions.

This last point would infer that the expression of the evolved physiological adaptation in a survival situation is in some way dependent on the structure of the environment as it is this part of the Australian scene that has changed so markedly in the past century because of the presence of European man and his agricultural and pastoral practices. But it is possible to see the changes induced by man's activities as being merely the culmination of a long period of environmental change which commenced some time in the Pliocene. During this period the biological part of the environment has changed from forest or woodland to open woodland and shrub understorey to open scrub-grassland or hummock grassland. In this context it is appropriate to consider ecophysiological responses as the end product of a long evolution in response to aridity which has

manifested itself principally in terms of water deficit accompanied by a simplification of the vegetational component of structure of the environment, i.e., the quokka on Rottneest Island is the analogue of what has happened over a longer period in the continent.

The fossil record suggests that as the floral composition and vegetational structure change, there appeared first a radiation of marsupials culminating in the evolution of very large species which in the recent past was terminated by widespread extinctions (Wells 1978). In view of the faunal reduction following these extinctions, one might ask whether adaptations of an ecophysiological nature have allowed persistence or whether other kinds of adaptation have been more important (Main and Bakker 1980).

Aspects of this problem have been discussed by Main (1978) in terms of how a species perceives the environment. The perception will be different for each species depending on its degree of adaptation. For example, a hot-arid climate may not be stressful to a species with a well-developed capacity to produce concentrated urine, which possesses a reflective coat or lives in a habitat which provides a heat refuge (e.g. *Macropus rufa* or *Macropus robustus*), but a similar environment would certainly be inadequate for any species which lacked such adaptive traits. In this way it is possible to see physiological performance as contributing to the ability to occupy specific habitats, but one needs to relate physiological capacity in a more general way to the field and the general ecology of a species. Thus one needs a bridge between ecophysiology and ecology and it seems that a conceptual framework is provided by the fundamental niche of Hutchinson (1957), conceived as a set of states of environmental variables permitting species to exist indefinitely.

The relevance of niche theory

In the context of ecophysiology we determine the states by laboratory or field measurement, and so may define the fundamental niche as an n-dimensional hypervolume or space which encloses all the environmental states that a species can tolerate and persist in indefinitely. In the presence of other species with which there are biological interactions, a species occupies a realized niche which differs from the fundamental niche. Kinnear and Main (1979) discussed these concepts with respect to nutrition.

In several papers (Main 1978, Kinnear and Main 1979, Main and Bakker 1980) it has been proposed that ecophysiological findings, when they establish limits of performance, really delimit boundaries of the n-dimensional hyperspace that is the Hutchinson fundamental niche. These measurements describe the conditions which would limit existence of each species if biological interactions (eg. competition) did not occur. In the absence of competition one might expect the fundamental niche to equate with the realized niche, i.e. the conditions under which the species is actually found e.g., the quokka on Rottneest. This is an unusual case and more realistically one might expect that biological interactions would lead to the occupancy of only part of the fundamental niche, i.e., the realized niche is less than the fundamental, e.g., the quokka in its mainland habitat.

It has already been mentioned that in Australia there has been considerable extinction in the recent geological past, and one might expect distribution of the survivors of this extinction to have ranges approximating to their fundamental niche because competition has been reduced. For example, the two species of grey kangaroo might have their ranges in the north-west and north-east determined by the fundamental niche of each species, but in the south-east *M. fuliginosus* may be restricted by competitive interactions with *M. giganteus* which is similarly limited on the south and west side of its range (Main 1978). Considering the significant answers which might be obtained by studying these species, we know surprisingly little of the ecophysiological responses of each.

In the field however, factors additional to physiological capacity appear to be important and in the face of a perceived stress an animal seems, to respond initially by committing the fewest resources to its relief generally by avoiding the stress in a behavioural way (Kitchener 1972). In the event that this is not successful, then progressively more and more resources are committed by way of physiological responses and then acclimation. The ultimate stage in the resource commitment is when part of the genotype is devoted to the heightened development of morphological and physiological attributes which permit existence in the continued presence of the stress, i.e. the organism adapts at the morphological and physiological levels. In the foregoing series, behavioural response are reversible at very little cost; physiological responses are more costly to reverse, for example, should evaporative cooling be used in temperature control when the replacement of water lost may be very difficult. On the other hand, once genetic resources are committed, change is in the order of generations and so is not likely to be rapid and reversibility is unlikely. Enhancement of physiological capacity to tolerate stress by genetic change is only likely to arise under a long-term régime of stress and selection.

Responses to aridity

In Australia, ecophysiological stressful events are mostly associated with aridity. Earlier (Main 1973) I discussed how arid environments are a composite of favourable and unfavourable environments which may be dispersed in time and place. Periods of favourableness vary in duration and amplitude as do the periods of unfavourableness or drought. In such an environment persistence as a population is only possible if the favourable periods are exploited by restoring population size and the unfavourable periods withstood because of behavioural avoidance or physiological tolerance. Such a system ceases to work when favourable periods are too short or the unfavourable periods exceed the generation time or life span of a species. Thus an arid-adapted species has to adapt to two sorts of environment which are quite different and for which adaptations may conflict. For example, a lowered metabolic rate may conserve water during drought but it would also produce delayed growth and hence development to sexual maturity would be longer, a disadvantage when population size is to be restored during favourable periods of short duration; or kidneys which can excrete concentrated

urine are advantageous during drought but when there is a surfeit of water in and on plants the kidney must be able to excrete the excess. The physiological adaptations which we see today result from long-term trends in aridity, the duration and amplitude of favourable and unfavourable periods, and the physiological and other compromises with which the species has responded to the periods of abundance and scarcity of resources.

The role of habitat

Southwood (1977) has discussed habitat in a general ecological context as the template of ecological strategies and develops a matrix for assessing reproductive success in terms of breeding "now" or "later" and "here" or "elsewhere". He then proceeds to discuss in terms of quantitative characters the components of habitat, these being heterogeneity in time (favourable or unfavourable), predictability (predictable, unpredictable, ephemeral), heterogeneity in space (patch characteristics with respect to food gathering or migration, and patch characteristics with respect to patch size and interpatch space, i.e. isolation) (Southwood 1977, Figs 6-9).

If ecophysiological capacities require a structured environment for successful expression, then the suggestions of Southwood appear to provide the necessary framework within which to interpret reproductive tactics of currently-surviving macropods along with their physiological adaptations and their use of habitat. Thus it would appear that ecophysiological capacities and habitat resources can be linked in a way which is potentially useful for devising management strategies, particularly if we think of the aims of management as being analogous to evolutionary success as conceived by Slobodkin (1972).

Evolutionary success can be gauged in two ways, after some have failed to survive, i.e. retrospectively, or as Slobodkin (1972) has suggested, by assessing the probability of a population surviving in the future, those more likely to survive having the greater measure of evolutionary success. The probability of survival will depend on having some assessment of the stressful situations that are likely to arise in the near future (more likely when they occur in the same season every year or when changes follow a trend and are not irregular, intense or sudden), and when the organism has the behavioural, ecological and physiological adaptations to meet the problem. Slobodkin (*op. cit.*) also points out that "high abundance and high reproductive rate are of evolutionary value in themselves only in situations in which there is a high degree of unpredictability expected in the environment." This is so because if physiological and behavioural adaptations fail, the organisms in a population can only ensure persistence by reproducing as rapidly as possible when conditions are favourable.

In the sense of the fundamental niche of Hutchinson, aspects of the sets of environmental states have been determined for macropods on five broad fields of study, namely, behaviour, nutrition, water and electrolyte balance, heat tolerance and reproduction. Within each of these fields of study there are numerous adaptive responses but none occurs in all surviving species so far analysed, nor are the adaptive

responses of the same magnitude even in species apparently subject to the same environment, which poses the question, why is this so?

In terms of Slobodkin's concepts the surviving arid land macropods appear to have assessed the future in two ways: (1) with respect to shelter: (a) that vegetation will continue to provide cover—(agile wallaby, hare wallaby, grey kangaroo and tammar) (b) that vegetation will not continue to provide cover and so electing to shelter elsewhere, e.g. in rock shelter—(euro, rock wallaby,) or evolving a reflective coat—(red kangaroos); (2) with respect to food quality: (a) those assessing that quality will remain high and retaining a little-modified gut and eating moderate to good quality diet—(red kangaroo, agile wallaby,) and (b) those assessing quality as being low and fibrous and whose gut is highly modified morphologically for fermenting fibrous diets: these are capable of recycling urea—(euro, grey kangaroo, hare wallaby, tammar).

In terms of Southwood's concept all those macropods that breed continuously are breeding "here" and "now", and in terms of the quote from Slobodkin, cited above, are indicating that, to them, the environment is unpredictable, which fits with Southwood's concept of habitat being favourable or unfavourable in time as well as being predictable or unpredictable. Macropod species recognise heterogeneity in space in different ways. Some species, e.g. red kangaroos and to some extent grey kangaroos, leave unfavourable patches and move to favourable ones, i.e. are nomadic, while other species, e.g. euro, hare wallaby, tammar, remain in their shelter sites in unfavourable times but may increase their foraging range. Those species depending upon structural vegetation for shelter will have their patches become progressively less favourable as successions proceed and the vegetation matures and dies or is replaced by plant less suitable as cover. In such cases the adults do not move but, during their occupancy of the patch, juveniles in excess of the carrying capacity of the patch have been produced and these act as explorers for and potential colonisers of unpopulated patches at the right stage for colonisation, e.g. mainland quokka (Christensen and Kimber 1975).

Environmental predictability

The question revolves around both the intensity of the unfavourable periods, i.e. the amplitude of the swing from favourable to unfavourable, and the periodicity of the recurrence of favourable or unfavourable. For example, annual summer drought has a fixed period of recurrence and so is predictable but may vary from year to year in intensity, i.e. amplitude. In arid regions generally, failure of rainfall and consequent absence of fresh plant growth may lead to long-term droughts which not only extend over several summer and winter seasons but may also persist for several years. In such cases the recurrence of drought can be regular or irregular and at intervals of several to many years. This is an aspect dealt with Slobodkin and Rapoport (1974) who classify perturbations as expected (e.g. seasonal heat or drought) or unexpected—the former being those within the animal's repertoire of responses and the latter outside them. In this sense expected perturbations can easily be accommodated within the

evolved behavioural or physiological capacities of the animal. Unexpected perturbations are those for which there are no evolved responses; if they occur with some regularity, then selection will lead to evolved capacities to handle them.

These authors suggest that it is the periodicity, expressed in terms of the expected life span, of the same environmental perturbation which results in a spectrum of adaptive responses ranging through behavioural, physiological, acclimation mechanism to morphological change. The extant macropod species are successful in one sense used earlier and it is of interest to see how their evolution and adaptations to unpredictable environments fit the above schema. In keeping with the ideas of Slobodkin & Rapoport (1974) on selective forces and responses we would expect seasonal perturbations to be experienced by all animals throughout their life span and they would respond with superficial behavioural or physiological adjustments. Droughts may or may not be experienced by all animals during their life span, yet when they are experienced they may call for a more intense and sustained response than is required to survive seasonal perturbations. Under such circumstances one might expect acclimation or enhanced physiological capacity such as metabolic depression, increased concentrating capacity of the kidney, an ability to recycle urea, and significant morphological modification might be selected. In this regard one would interpret the spectacled hare wallaby *Lagorchestes conspicillatus* and the euro *Macropus robustus* as being highly evolved.

In the Australian environment fire is unpredictable; also its effects exacerbate the deleterious effects of seasonal or more extended droughts, but its effects probably do not call forth any new responses. Of the macropod marsupials studied, the habitat of the hare wallaby *L. conspicillatus* is most seriously affected by fire because the *Triodia* tussocks used for shelter are very inflammable. Destruction of cover should exacerbate the effects of the irregular but prolonged droughts which occur over its range. The adaptive responses of the hare wallaby are consistent with those expected from the reasoning of Slobodkin and Rapoport (1974) in so far as the hare wallaby has the highest relative medullary thickness of kidney and the maximum urinary osmotic pressure of those macropods studied (Main and Bakker 1980).

The testing of the foregoing theoretical expectations and their application to macropod species generally is not possible with our present knowledge. Undoubtedly the integration of ecophysiological findings with other aspects of the ecology requires an attention to the quantitative aspects of the habitat (Southwood 1977). Moreover, in order to account for the different adaptive responses of different species to the same environmental perturbations it is necessary, following Slobodkin & Rapoport (1974), to relate the probability of encountering the perturbations to the expected life span of the species under study. Should such an ambitious goal be achieved, ecophysiological studies will become a significant and integrated part of ecological and evolutionary studies of populations. Moreover, such an integrated approach affords the opportunity for wide-ranging comparative studies for which the present ecophysiological and ecological knowledge is unfortunately inadequate. However, this inadequacy cannot be ignored because

the development of strategies and tactics for the management of macropod species in conservation reserves of limited size depends on integrated laboratory and field studies somewhat on the lines of Prince (1976) but with attention to the components of habitat which contribute to amelioration of the stressful effects of drought such as shelter as a heat refuge or nitrogen status of plants or access to fermentable energy so that urea can be recycled.

Conclusion

It is apparent that many of the results arising from work on the quokka on Rottnest Island have given rise to interpretations which are applicable to and testable on macropods generally. The findings and interpretation show a congruence with the general theories proposed by Hutchinson (1957), Slobodkin and Rapoport (1974) and Southwood (1977), and can be readily interpreted within such a framework. Such a result is ample justification for the selection of the Rottnest Island quokka as the model macropod marsupial, as mentioned in the introduction. Moreover, it seems clear that in terms of usefulness as a model, the quokka has not been superseded.

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Geological research on Rottnest Island

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Abstract

Rottnest Island forms part of a chain of limestone islands and reefs marking former Quaternary shorelines. It is composed of Pleistocene to Holocene dune limestone (Tamala Limestone), late Pleistocene coral-reef limestone (Rottnest Limestone), mid-Holocene shell beds (Herschell Limestone), and superficial Holocene deposits.

The Rottnest Limestone coral reef grew about 100 000 years ago when sea level was relatively at least 3 m higher than today. Separation of the island from the mainland occurred about 6 500 years ago as sea level rose near the end of the Holocene Flandrian transgression. This was followed by the extinction of most animal and plant species.

The Holocene transgression reached its peak about 2.6 m above present sea level some 5 500 to 5 000 years ago. Two earlier brief still-stands occurred successively about 0.5 m and 1.2 m above present sea level. The final regression to modern sea level may have been of tectonic (rather than eustatic) origin.

A lens of potable groundwater situated west of the salt lakes has been developed to service settlements on the island.

Introduction

The first detailed geological studies on Rottnest Island were carried out by Teichert (1950). His work dealt mainly with the eastern part of the island and the evidence displayed there of Quaternary sea-level changes. Hassell and Kneebone (1960) studied the island as a B.Sc. Honours project at the University of Western Australia, and their work was summarized by Glenister, Hassell, and Kneebone (1959).

Research by the Geological Survey of Western Australia at Rottnest began in 1976 as part of an investigation into the island's groundwater potential (Playford 1976, Playford and Leech 1977). This work further elucidated the Quaternary geology and geological history and succeeded in finding a source of potable groundwater. Since then work by the Geological Survey has continued, and this paper summarizes present knowledge of the geology of the island.

Geomorphology

Rottnest is the largest island in a chain of limestone islands and reefs on the continental shelf opposite Perth. They are composed of dune limestones marking former mainland shorelines which migrated as sea level rose and fell successively during interglacial and glacial periods of the Pleistocene.

Rottnest Island is characterized by alternating limestone headlands and bays with wide sandy beaches backed by Holocene sand dunes. The coast is fringed by shoreline platforms and offshore "reefs" formed by marine planation of Pleistocene dune limestone and encrusted with thin layers of coralline algae and corals. The Pleistocene dune limestone which underlies most of the island is prominently exposed on the headlands; in the interior it is mainly obscured by a veneer of residual or wind-blown sand.

Salt lakes occupy about 10% of the area of the island. They have elongate-ovoid to sub-circular shapes, and are believed to overlie dolines formed by rainwater solution of the limestone and subsequent

collapse of cave systems during low sea levels of the Pleistocene. The dolines were subsequently largely filled with Holocene sediments. The prominent "blue holes" of the Houtman Abrolhos appear to have a similar origin (Playford and Leech 1977). Water levels in the lakes rise to about mean sea level in winter and fall more than a metre in summer. Some of the smaller lakes dry out completely at the end of summer, forming a salt crust, while the larger lakes commonly have late-summer salinities exceeding 150 000 mg/L.

Geology

Rottnest Island is composed of Pleistocene to middle Holocene dune limestone (Tamala Limestone), with a thin intercalation of Late Pleistocene coral-reef limestone (Rottnest Limestone), overlain by thin middle Holocene to modern deposits: shell beds (Herschell Limestone), dune sand, beach sand, swamp deposits, and lake deposits. The surface geology is illustrated on Figure 1.

Rock Units

The *Tamala Limestone* is a unit of eolian calcarenite composed of wind-blown shell fragments with variable amounts of quartz sand, and is characterized by large-scale eolian cross-bedding. Over most of the island the formation is mantled by residual quartz sand derived by weathering of weakly lithified sandy limestone.

The Tamala Limestone is known from coastal areas and islands extending from Shark Bay to the south coast, and it ranges from Pleistocene to Holocene in age. At Rottnest the oldest exposed part of the formation probably dates from the Riss Glaciation and the following transgression; the youngest is Holocene, laid down during the Flandrian transgression. The formation contains some prominent soil horizons marking interruptions in dune building. They are underlain by calcrete layers, often associated with abundant fossil root structures (rhizoliths).

Drilling suggests that the Tamala Limestone below Rottnest is about 115 m thick, extending to 70 m

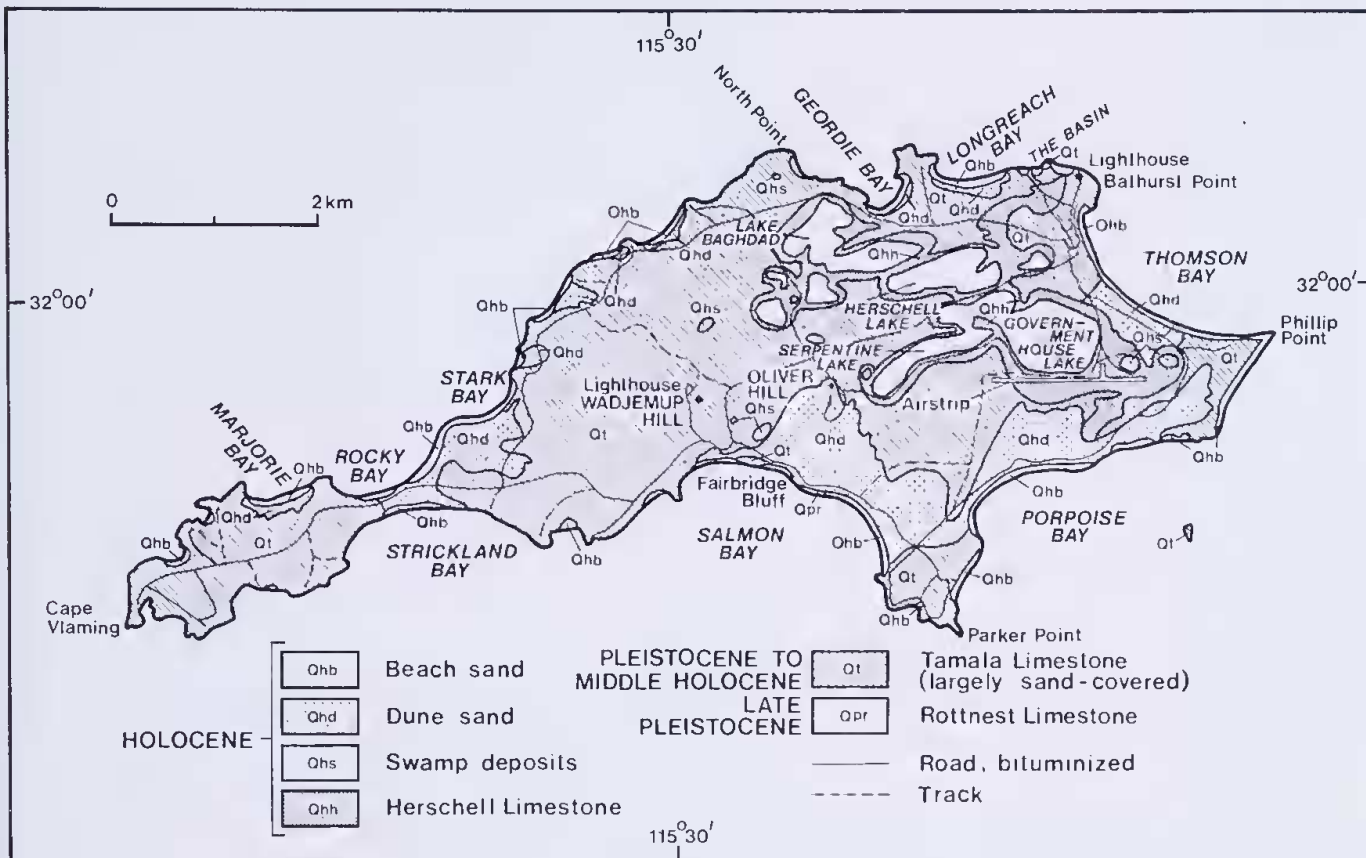


Figure 1.—Geological map of Rottne Island.

below sea level, where it overlies older Pleistocene or Tertiary sands.

The *Rottne Limestone* (Fairbridge 1953) is a Late Pleistocene unit of coral-reef limestone and associated shelly (gastropod-rich) limestone exposed at Fairbridge Bluff in Salmon Bay. The formation is overlain and underlain by Tamala Limestone and is believed to represent a marine tongue intercalated in that formation. The total exposed thickness of the Rottne Limestone is 3 m.

The coral fauna is dominated by branching species of *Acropora*, a genus which today is not known further south than the Houtman Abrolhos, 350 km to the north. Its occurrence in the Rottne Limestone thus indicates warmer-water conditions when the reef grew than those prevailing in the area at present. Coralline algae (*Lithothamnium*) also made substantial contributions to the reef framework.

The Rottne Limestone has been dated by uranium-thorium methods as $100\,000 \pm 20\,000$ years old (Veeh 1966), and it thus dates from the last Pleistocene interglacial period.

The *Herschell Limestone* is a unit of Holocene shell beds with intercalated lime sand and marl which is exposed around the margins of the Rottne salt lakes. It overlies and abuts the Tamala Limestone and is overlain by superficial Holocene deposits. The unit is at least 3 m thick, and it is believed to have been deposited in subtidal to intertidal environments.

The fauna of the formation is dominated by many species of bivalves and gastropods (Kendrick 1977).

All are living species, but some no longer live in the Rottne area.

Radiocarbon analysis of shells in the formation gives dates of around 5 500 to 5 000 years (Tamers *et al.* 1964, Deevey *et al.* 1959), with one anomalous date of about 3 800 years (Deevey *et al.* 1959), which is probably too low because of contamination by younger carbonate. Playford and Leech (1977) concluded that the Herschell Limestone was probably deposited about 5 500 to 5 000 years ago, at the peak of the Holocene transgression in this area.

Superficial deposits of Holocene age mantle most of the island. They consist of dune sand, beach sand, swamp deposits, lake deposits, and residual sand (largely derived from the Tamala Limestone).

The swamp deposits were laid down in a series of small fresh- and brackish-water swamps. They consist of thin layers of marl, lime sand, peat, and algal sediments. The palynology of these deposits was studied by Hassell and Kneebone (1960), who showed that pollen from tuart, jarrah, marri, white gum, sheoak, peppermint, banksia, and zamia palm occur at depths of a metre or more below the surface. This shows that the typical tuart-woodland association of the mainland occurred on Rottne in the past, although none of the species occur there naturally today. Playford and Leech (1977) deduced that this floral association (characteristic of mainland coastal areas opposite Rottne) probably disappeared soon after Rottne separated from the mainland. At the peak of the Holocene transgression the land area was much smaller than that of

the island today (Fig. 3) and the effects of salt spray (inimical to tuart woodland) were consequently more extensive.

The modern salt-lake deposits consist of algal and evaporitic sediments. In Government House Lake they include columnar algal stromatolites growing in water up to about 3 m deep.

Sea-level changes

The most notable feature of the surface geology of Rottnest Island is the excellent evidence there of Quaternary sea-level changes. This is in the form of (a) elevated marine deposits, (b) elevated shoreline platforms and notches, and (c) subaerial features which now extend below sea level.

The Department of Lands and Surveys has recently carried out levelling at Rottnest on behalf of the Geological Survey in order to better relate the various elevated features to their present-day equivalents. Although further levelling is desirable, some preliminary amendments are made in this paper to the approximate elevations assigned by Playford and Leech (1977) to the various emerged features.

The levels of modern shoreline platforms were determined at three localities adjoining the eastern half of the island; these are -0.402 m at The Basin -0.428 m at Fairbridge Bluff, and -0.480 at Thomson Bay (near the hotel). They average about 0.44 m below mean sea level (A.H.D.), which is 0.1 m below mean low water level, and would be exposed about 1% of the time each year (D. F. Wallace, pers. comm., 1982). Elevated shoreline platforms and associated notches, and the top of the fossil coral reef, have been related to this level in order to deduce the amount of emergence that has occurred.

Elevated marine deposits: The fossil coral reef of the Rottnest Limestone extends to 3.02 m above the adjoining shoreline platform. Consequently it is concluded that sea level relative to Rottnest during the last interglacial was at least this amount higher than it is today. However, this is a minimum figure, as the top of the coral reef could have grown in water several metres deep.

The highest marine shell beds of the mid-Holocene Herschell Limestone extend to about 2.15 m above mean sea-level or 2.6 m above the modern shoreline platforms. This is the same level as the highest of the emerged shoreline platforms, and both apparently formed at about the same time, some $5\,500$ to $5\,000$ years ago.

Elevated platforms and notches: Three levels of elevated shoreline platforms and notches are recognised at Rottnest Island: an upper level at about 2.6 m, an intermediate level at about 1.3 m, and a lower level at about 0.5 m above the modern shoreline platforms (Fig. 2). These are the "3 m, 1.5 m, and 0.7 m" levels of Playford and Leech (1977).

The upper (2.6 m) level is visible at many places around the coast, and especially around the salt lakes. The intermediate (1.3 m) and lower (0.5 m) levels are best preserved around the lakes, in the form of notches with weakly developed narrow platforms (Playford and Leech 1977, Figs. 15-17). The intermediate and lower levels are rarely preserved around

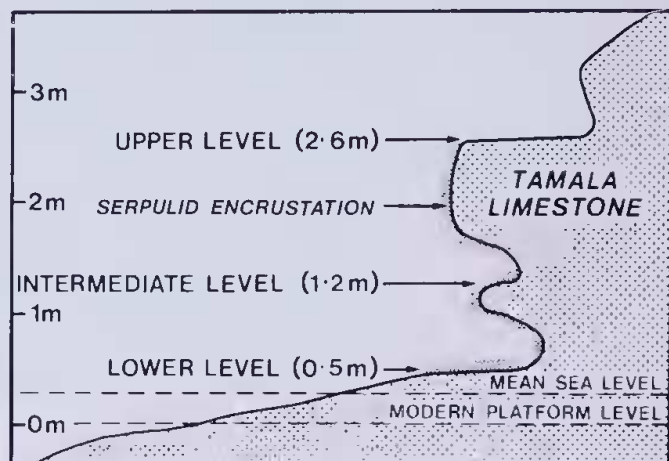


Figure 2.—Diagram illustrating elevated shoreline platforms and notches around the Rottnest salt lakes. The elevations of these features are related to the average elevation (0.44 m below mean sea level) of modern shoreline platforms around the island.

the coast of the island, as there they are subject to modern wave attack.

At many localities a layer of serpulid worm tubes is discontinuously preserved encrusting the two lower notches and platforms, and extending up to the upper-level platform (Fig. 2). The limestone on which the serpulids grew is commonly intensely bored by marine organisms. Some pockets of bivalves and gastropods (species also found in the Herschell Limestone) are associated with the serpulid layer, and there are also some encrustations of bryozoans and small solitary corals. These organisms grew under subaqueous marine conditions and once formed an essentially continuous crust over the surface below the upper-level platform. From this it is clear that the two lower notches and their associated platforms were already in existence when the transgression reached the upper (2.6 m) level. Each of the three levels is believed to represent a still-stand of no more than a few hundred years as relative sea level rose through three steps to its final peak about $5\,500$ to $5\,000$ years ago. The regression following this peak must have been abrupt; otherwise the relatively fragile serpulid crust would have been removed by marine erosion.

Subaerial features extending below sea level: Lithified dune limestone of the Tamala Limestone extends below sea level around the coast of Rottnest, and may reach depths of 70 m or more. Most of the formation is thought to have accumulated when sea level was considerably lower than it is today.

At several localities around the coast solution pipes in the Tamala and Rottnest Limestones can be seen extending below sea level, testifying to sea levels lower than at present when they formed. As previously mentioned, the salt lakes probably overlie major dolines formed by rainwater solution and collapse during the low sea-level stands of the glacial periods.

Origin of sea-level changes

The major changes of sea level affecting the Swan Coastal Plain and adjoining continental shelf during the Pleistocene resulted from eustatism

associated with waxing and waning of the continental ice sheets (see discussions in Playford *et al.* 1976 and Playford and Leech 1977). However it is doubtful that the Holocene "high sea levels" evidenced at Rottnest and elsewhere along the Western Australian coast were truly eustatic (i.e. world-wide events), as had been postulated by Teichert (1950), Fairbridge (1958 and 1961), and Hassell and Kneebone (1960).

As pointed out earlier, there was apparently an abrupt fall in sea level at the close of the still-stand evidenced by the upper-level platform. This prompted Playford and Leech (1977) to suggest the possibility that it had a tectonic origin.

However, it still remains to be shown whether this relative fall in sea level during the mid Holocene was of regional or local extent. If it was regional, did it result from world-wide eustatism, epeirogenic uplift, global changes in the geoid, or some other cause? If the relative fall in sea level was of local extent, did it result from movement along a fault on or adjoining the continental shelf, possibly triggered by rapid loading of water during the Flandrian transgression, or was it associated with movement along the Darling Fault? The answers

to these questions must await further precise work to correlate emerged platforms and other features at Rottnest with similar features in Western Australia and elsewhere in the world.

Quaternary geological history

The foundations of Rottnest Island may have been originally localized by a sand shoal, perhaps associated with an uplifted area in underlying Tertiary rocks. Calcareous sand dunes accumulated in the area during the Pleistocene to form the Tamala Limestone. This formation had a long history of dune building, soil development, and karstification during successive glacial and interglacial periods of the Pleistocene. The oldest dune limestones exposed on the island may date from the Riss Glaciation and the ensuing transgression, but older Pleistocene parts no doubt occur in the subsurface.

During the Riss-Wurm interglacial a coral reef grew on the dune ridge of Tamala Limestone. Sea level fell progressively during the Wurm glaciation, reaching its lowest level of about 130 m below its present level some 18 000 years ago. The coastline was then about 12 km west of Rottnest (Fig. 3), and the old dune and reef limestones stood as a

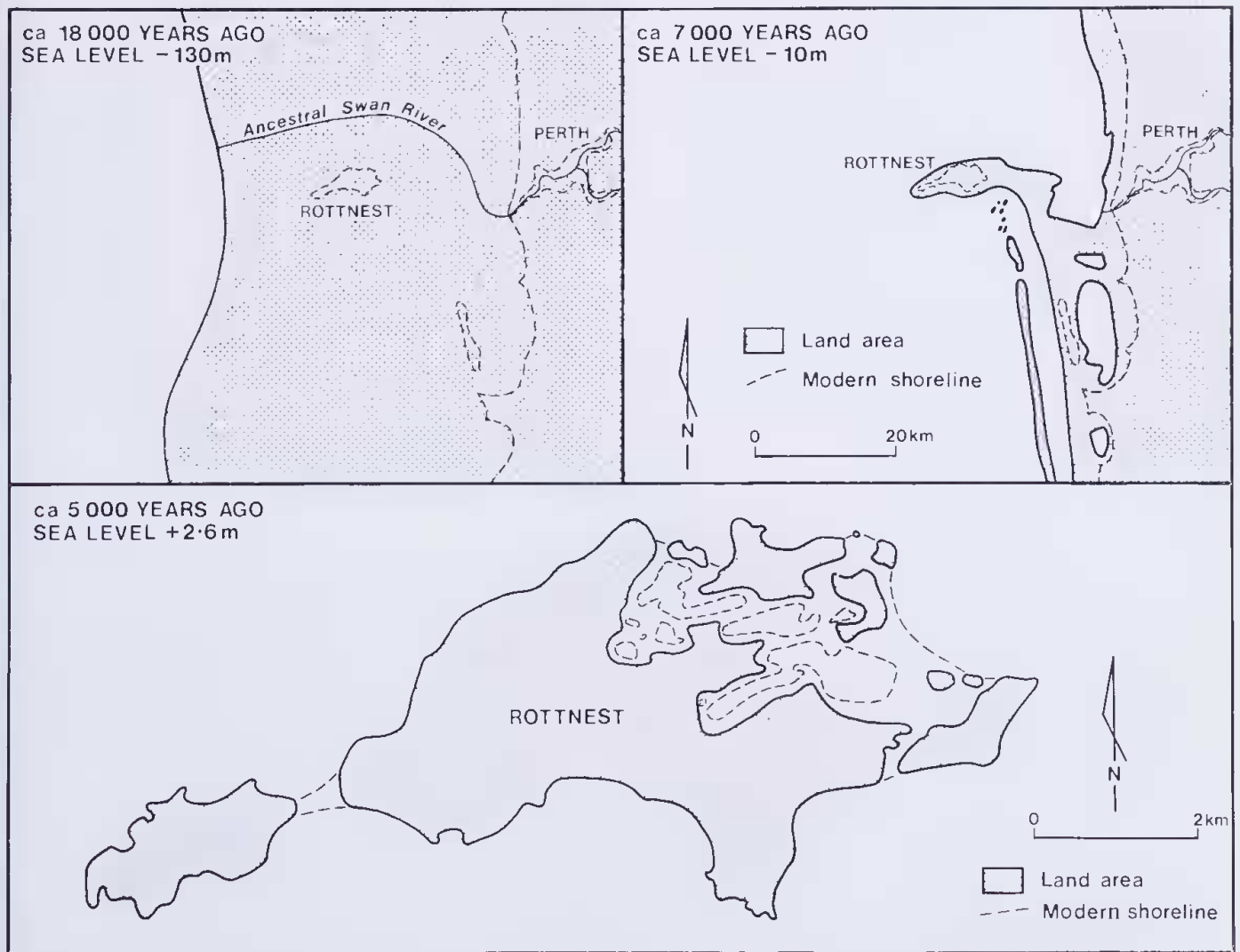


Figure 3.—Palaeogeographic maps illustrating shoreline changes in the Rottnest-Perth area during the Late Pleistocene and Holocene.

conspicuous "mountain" high above the surrounding plain. The ancestral Swan River then flowed out to sea northwest of Rottnest, where it joined a submarine canyon (the Perth Canyon) incised into the continental slope. Strong karst solution proceeded in the limestones, with the formation of the large dolines that were afterwards to localize the modern salt lakes.

Sea level rose rapidly during the Holocene Flandrian transgression. Dune sands of the younger Tamala Limestone accumulated on the Rottnest platform as part of a belt extending through the present Carnac, Garden, and Penguin Islands. As the sea rose towards its present level, Rottnest remained in connection with the mainland along this belt of dunes (Fig. 3). The island probably separated about 6 500 years ago. Major changes in the land flora and fauna of the island followed this separation; only a few of the original plants and animals survived to the present day.

The maximum submergence at Rottnest, to about 2.6 m above present sea level, probably occurred some 5 500 to 5 000 years ago. The area of the present salt lakes then formed arms of the sea between more than 10 separate islands (Fig. 3). Prolific molluscan faunas lived in the warm shallow waters between these islands, and their close-packed shells now form much of the Hershell Limestone.

There were two brief intervals of still-stand, totalling no more than a few hundred years, at about 0.5 m and 1.2 m above present sea level, as the sea rose to its peak (2.6 m) level. Notches and narrow shoreline platforms were eroded at each of those levels.

There was an abrupt fall in sea level, or the Rottnest area was suddenly uplifted, about 5 000 years ago, when the sea attained its present level relative to the island. The area of the present salt lakes remained in connection with the sea for some time, but it was eventually cut off by the accumulation of beach ridges and sand dunes. Superficial deposits continued to accumulate after that time, but there have probably been no major changes in the configuration of the island for the past 2 000 or 3 000 years.

Hydrogeology

The supply of domestic water in sufficient quantities and at reasonable cost was a major problem at Rottnest for more than 60 years. After World War II most drinking water came from sealed catchment areas and (1961 to 1976) by barge from the mainland. However, when a decision was made in 1975 to build a second settlement at Longreach and Geordie Bays, it was clear that some new water source would have to be found, either

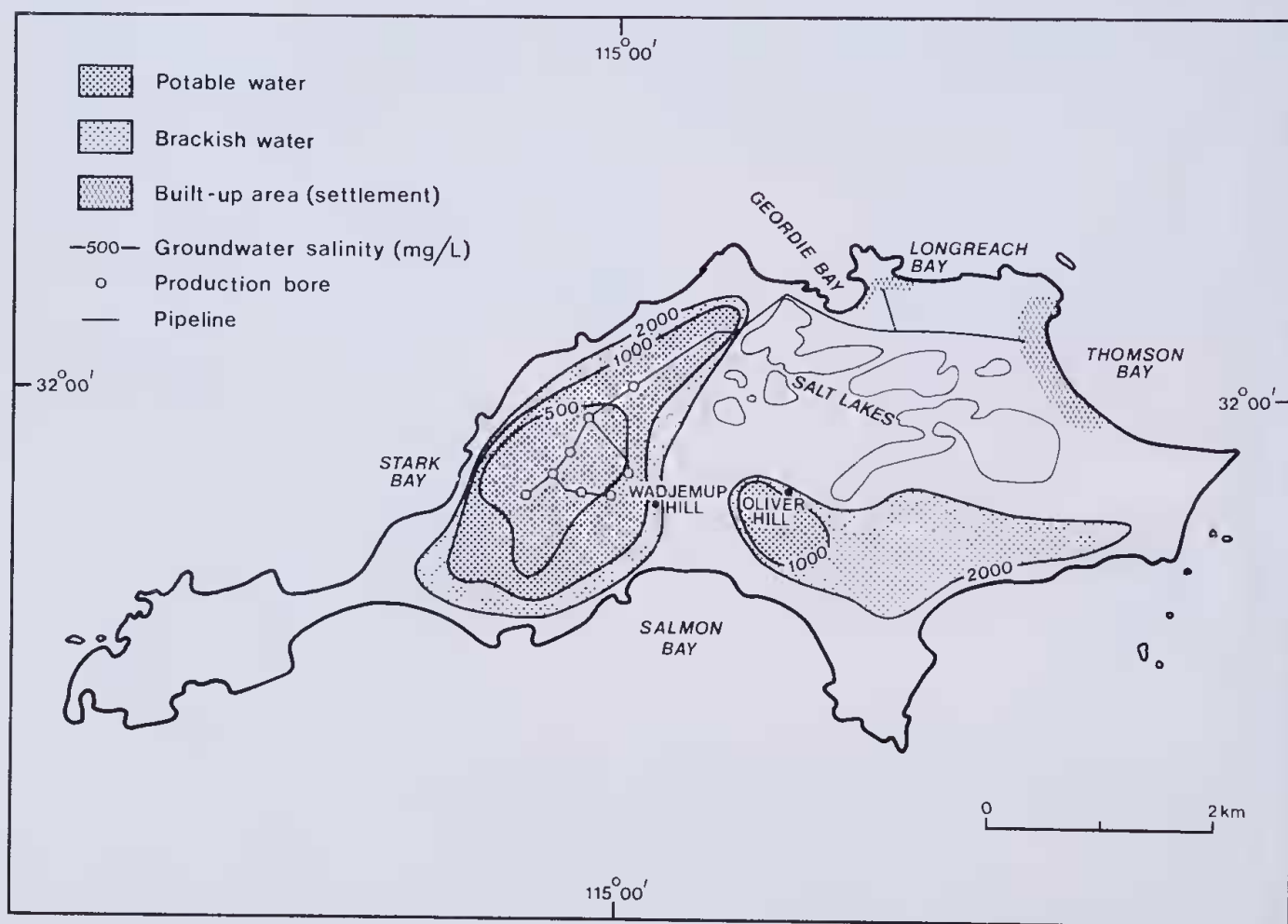


Figure 4.—Map showing the locations of fresh and brackish groundwater lenses below Rottnest Island.

from underground aquifers or by building an undersea pipeline from the mainland.

There had been a long-held belief that secure sources of potable groundwater could not be found at Rottneest. This was because in 1911-12 an artesian bore drilled on the island had recovered nothing but salt water, and shallow bores and wells around the Thomson Bay settlement yielded only brackish to very saline water. The Geological Survey's re-evaluation of the groundwater prospects in 1976 showed that the chances of finding potable artesian water were almost nil, but that the most prospective part of the island for shallow groundwater, situated below the high ground west and south of the salt lakes, had never been tested. It was suggested that these areas could yield significant volumes of domestic-quality groundwater, and that accordingly they should be drilled as soon as possible (Playford 1976). The prediction was proved correct; two lenses of fresh (less than 1 000 mg/L) to brackish (1 000 to 2 000 mg/L) water were defined in these areas (Fig. 4). The area west of Wadjemup Hill contained sufficient reserves of potable water in a lens up to 10 m thick in the Tamala Limestone to be developed for use in the settlements (Playford and Leech 1977). The necessary bores and a pipeline were completed within a few months, and production began in October 1976. Since then exploitation of the groundwater lens has proceeded without major problems, and it is estimated that abstraction in each year has averaged only 9% of the annual recharge from rainfall.

Supplies from this source together with those from existing sealed catchments should be sufficient to meet the essential potable water needs of the island for many years. The other lens, in the Oliver Hill area, contains mainly brackish water, but it has potential for development to improve the second-class water system (for ablution and sanitary purposes), which at present is supplied by saline wells in the settlement areas.

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Salmonella on Rottneest Island: Implications for public health and wildlife management

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Abstract

Salmonella infections of 40 serotypes have been studied in humans, a wild marsupial (the quokka, *Setonix brachyurus*), birds and the environment on Rottneest Island (W. Australia). The vegetation of the island is very disturbed and during the hot and dry summer the quokkas suffer starvation. Up to 100% of the quokkas are infected throughout the summer (median rate of excretion 10^{3.5}/g of faeces) although there is no evidence of disease. There is widespread environmental contamination and consequent infection of birds and humans. The situation has been studied in detail in relation to public health and wildlife management.